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A COMPARISON OF THE DIVERSITY AND COMPOSITION OF GROUND-ACTIVE SPIDERS IN MKOMAZI GAME RESERVE, TANZANIA AND ETOSHA NATIONAL PARK, NAMIBIA

A. Russell-Smith: Natural Resources Institute, University of Greenwich, Central Avenue, Chatham Maritime, Kent ME4 4TB, UK. E-mail: a.russell-smith@gre.ac.uk

ABSTRACT. Pitfall traps were used to census ground-active spiders in 12 different habitat types in protected savanna biomes in Tanzania and Namibia. With roughly equivalent trapping effort in the two areas, a total of 229 spider species and 40 families were trapped in Mkomazi Game Reserve and 151 species and 34 families in Etosha National Park. The family composition of the fauna of the two areas was similar, with Salticidae accounting for 17% (Mkomazi) and 14% (Etosha) of all species and Gnaphosidae accounting for 16% (Mkomazi) and 14% (Etosha) of the total. Other families that accounted for a significant proportion of species included Lycosidae (6–7%) and Zodariidae (6–7.5%). Despite the intensive trapping effort, there was no indication from species accumulation curves that a complete estimate of the spider species richness had been obtained from either area. The possible reasons for the differences in spider species richness and family composition in the two areas are discussed.

Keywords: Spider biodiversity, family composition, Etosha National Park, Mkomazi Game Reserve.

Although much is known about invertebrate diversity in temperate habitats, studies on species diversity in tropical ecosystems are more recent. A majority of studies have focused on tropical rainforest canopies because invertebrate diversity in them is so high. Very much less attention has been paid to invertebrate diversity in savanna areas, despite the fact that, broadly defined, savannas occupy more than twice the total land area of rain forests. This applies equally to research on spider diversity in tropical areas where the majority of reported work has been on forests (reviewed by Russell-Smith & Stork 1994).

In Africa, most inventories of savanna spiders have either been undertaken for purposes other than biodiversity assessment (e.g. Blandin & Celerier 1981; Russell-Smith 1981) or have been conducted over a limited time span or in a limited area (Russell-Smith et al. 1987; Lotz et al. 1991). There have been few attempts to census spider diversity over the full range of savanna habitats within a given area.

In this paper, assessments of spider biodiversity conducted as part of much larger surveys of invertebrate diversity in Mkomazi Game Reserve, Tanzania and Etosha National Park, Namibia are described. Both surveys censused spiders of the ground layer, field layer and tree canopies in the two sites but, for logistical reasons, most effort was focused on the ground layer fauna. Pitfall trapping in 16 habitats ranging from dry grasslands to woodland or dry forest in both areas was used to assess spider diversity over a three year period. Trapping effort was very similar in both areas and the results are thus directly comparable.

METHODS

Study areas.—Mkomazi Game Reserve in northern Tanzania lies at approximately 4° S and between 38° and 39° E, adjacent to the Kenya border and forming a southern extension of the much larger Tsavo (West) National Park in Kenya. The park covers an area of about 3600 km^2 and varies in elevation from 630–1600 m. It is bounded to the South by the Usambara Mountains, to the West by the East Pare Mountains and to the East by the Indian Ocean. Apart from isolated hills rising to 1600 m elevation, the land surface is a gently inclined peniplane falling gradually from ca 1000 m in the West to ca 700 m in the East. Rainfall ranges from 800 mm in the West of the reserve to 200 mm in the East and most of the rain falls in two periods, in March and April and October to December.

The vegetation of the reserve consists of a mosaic of woodland, bushland, wooded or bushed grassland and open grassland in which the boundaries between different vegetation types are often gradual and indistinct. Many of the wooded or bushy habitats are dominated by species of *Acacia* and *Commiphora*, either individually or as mixed stands and it is estimated that these may comprise some 70% of the total area of the reserve. Forest habitats are confined to isolated hilltops (principally in the West of the reserve), where dry montane forests are dominated by *Spirostachys africana* and *Brachylaena huillensis* and to a fringe of riverine forest along the Umba River in the East, dominated by leguminous trees of the genera *Afzelia*, *Albizia*, *Newtonia* and *Tamarindus*. Pure grassland is almost confined to low lying areas (locally known as "vleis") on black cracking clay soils which are subject to seasonal inundation. Grasslands vary in height from 25 cm or less in the dry season to almost 200 cm in perennial grasslands in the wet seasons.

Pitfall sampling was carried out in 12 distinct vegetation types as follows: Seasonally inundated grassland with *Acacia drepanolobium* on black cracking clay (vlei grassland), near Ndea Hill; Seasonally inundated grassland with *Acacia zanzibarica*, near Ngurunga; Grassland derived from montane *Spirostachys* forest, summit of Ibaya hill; Unburnt mixed grassland on foot slope, near Ibaya Camp; Unburnt *Acacia/Commiphora* woodland on lower hill-slope, near Ibaya Camp; Open *Acacia senegal* woodland, near Ndea Hill; Mixed riverine scrub, margins of Umba River; Mixed *Combretum* scrub, margins of Umba River; Mixed *Combretum* bushland, near Dindira dam; *Acacia senegal/A. nilotica* woodland, near Ubani; Dense *Dichrostachys cinerea* scrub, near Dindira dam; Montane *Spirostachys* forest, summit of Ibaya hill. These are listed in approximate order from habitats with the least tree cover to those with the greatest. Further details of these habitats can be found in Coe et al., 1998.

Etosha National Park is situated in the north of Namibia and lies along latitude 19° South between approximately 14° and 16° East longitudes. The park covers an area of 22,000 km^2 and is centred on Etosha pan, a very large area of seasonally flooded saltpan. The general land surface is extremely flat with isolated inselbergs to the south of the pan but with slightly larger hills in the extreme south and west of the reserve. Rainfall ranges from about 450 mm in the East of the reserve to about 300 mm in the West. Nearly all rainfall falls between November and April but is extremely erratic, with some years with less than 30 mm total rainfall.

The range of vegetation types within the reserve is, in many respects, similar to that in Mkomazi Game Reserve, with woodland, bush and grassland habitats which intergrade gradually with one another. Differences in the vegetation of the two reserves include the absence of true forest habitats from Etosha and the much greater area of grassland or bushed grassland habitats here than in Mkomazi. In general, closed woodland is confined to the higher rainfall area of the east of Etosha and open grassland habitats become more frequent towards the West. Open grassland is however, found throughout the reserve both on saline soils and on shallow soils on calcrete. Another difference is that *Commiphora* species are much less abundant in woodland and bushland in Etosha than in Mkomazi and *Acacia* species, although widespread and common, rarely dominate woodland and bush in Etosha. Further details of the vegetation of Etosha can be found in Le Roux et al., 1988.

Pitfall trapping was conducted in the following 12 vegetation types: *Terminalia/Combretum* woodland, Beisebvlakte and Oshivelo; *Terminalia/Spirostachys* woodland, Leeudrink; Mixed woodland, southeast corner of reserve; Open *Combretum/Kirkia* woodland on dolomite inselberg, Helio Hill; Dense shrub mopane bushland on calcrete, Natukanaoka and Otjivalunda; *Colophospermum/Combretum* bushland, Ombika and Ongava; Open shrub mopane bushland on loam, Bitterwater; Open *Colophospermum/Combretum* bushland ("Kaokoveld"), Oliphantsrus; Mixed shrub/low tree savanna, near rain gauge 17; Mixed *Acacia/Terminalia* shrub bushland, Duineveld; *Eragrostis/Ennapogon* grassland ("sweet grassveld") on calcrete, Okaukuejo; *Sporobolus/Odyssea* grassland, Andoni South and Andoni North. These are listed in approximate order from habitats with the greatest tree cover to those with the least. Further details of these habitats can be found in Le Roux et al. (1988).

Sampling Method.—In Mkomazi, diversity of ground-living spiders was studied with pitfall traps constructed from plastic coffee beakers each 7 cm in diameter and 10 cm deep. Traps were spaced at a minimum of 2 m apart and filled to a quarter of their depth with water to which a trace of household detergent was added. To reduce disturbance resulting from daily emptying, two plastic cups were placed one inside the other and only the inside cup was removed from the ground. Trap contents were removed onto a 1 mm mesh sieve and preserved in 70% ethanol for subsequent sorting and identification. Normally, traps were placed in three rows of 10 traps spaced 5 m apart, and left in the field for periods of either three or six days before emptying. The contents of the 10 traps from each row were pooled at each site sampled. Sampling was most intensive at the two sites close to Ibaya camp where pitfall traps were operated over six day periods in November 1994 and for six days in each month from April to August 1995. Samples from the remaining site were taken either over three days (vlei grassland near Ndea, grassland derived from montane forest on Ibaya Hill and open *Acacia senegal* woodland near Ndea) or six days (all remaining sites other than the last one) in April 1995 or January 1996. Samples were taken over three days in April 1995 and six days in January 1996 in the montane forest (site 12). Total trapping effort in Mkomazi was 7,200 trap days.

A similar system was used in Etosha except that traps were 10 cm in diameter and 9 cm deep. A killing fluid of ethylene glycol diluted to 50% with water was used. Here, traps were placed in four rows of 10 and were emptied after four days in the field. The catch from each row of traps was pooled. Sampling was carried out at the first 6 sites listed above in November 1996 and January, March, June and November 1997. Sampling from the second six sites listed was in March 1998 only. The total trapping effort at this site was 7,680 trap days. Voucher specimens of the Salticidae from Mkomazi Game Reserve are deposited in the Musée Royal de l'Afrique Centrale, Tervuren, Belgium while those for all other families remain in the author's collection. Voucher specimens of all spiders from Etosha National Park are deposited in the National Museum of Namibia, Windhoek.

RESULTS

Family and species richness and diversity.—The family composition of the spider fauna for the two study areas is shown in Table 1. In both areas, Salticidae and Gnaphosidae accounted for the largest proportion of spider species, each representing approximately 16%-17% of all species at Etosha and 14% of all species at Mkomazi. Other families that were well represented in both areas included Lycosidae (~ 6%− 7% of all species) and Zodariidae (~ 6.%−7.5% of all species). Corinnidae, Theridiidae and Thomisidae were well represented in traps at Mkomazi but were rare in traps in Etosha. Prodidomidae represented 9% of all species at Etosha but less than 2% in Mkomazi. The families Amaurobiidae, Clubionidae, Ctenidae, Hahniidae, Mimetidae, Miturgidae, Mysmenidae, Telemidae, Tetrablemmidae, Tetragnathidae, Theridiosomatidae and Uloboridae, 22 species altogether, were only recorded in traps at Mkomazi. Conversely, the families Ammoxenidae and Sicariidae, 7 species altogether, were only recorded from traps at Etosha. There were 78 more spider species and 6 more families recorded from Mkomazi Game Reserve than from Etosha National Park (Table 1).

Efficiency of trapping.—The conclusions drawn as to the differences in spider species richness between the two areas will depend to some extent on how complete the sampling effort was in each. The cumulative numbers of spiders trapped is plotted against the cumulative number of trap days for both sites in Fig. 1. While the rate of accumulation of new species trapped was always greater in Mkomazi than in Etosha, it is evident that in neither area does the curve for species accumulation over sampling effort approach an asymptote. However, the rate of species accumulation does appear noticeably lower in Etosha than in Mkomazi from 5,000 trap days to 7,600 trap days.

DISCUSSION

Despite the relatively intensive sampling effort in both of the study areas, it is evident from Fig. 1 that the census of species was far from complete. Although this may, in theory, mean that the difference between the two sites in spider species richness is less than suggested in this study, there is little reason to suppose that species richness would actually be higher at Etosha than at Mkomazi.

The family composition of the ground-active spider faunas in both areas studied is fair-

Table 1. The family and species composition of spiders from pitfall traps in Etosha National Park, Namibia and Mkomazi Game Reserve, Tanzania.

Etosha National Park, Namibia		Mkomazi Game Reserve, Tanzania	
Family	Species	Family	Species
Agelenidae	3	Agelenidae	1
Ammoxenidae	6	Amaurobiidae	3
Araneidae	0	Araneidae	6
Atypidae	1	Atypidae	1
Barychelidae	1	Barychelidae	2
Caponiidae	1	Caponiidae	2
Corinnidae	1	Clubionidae	1
Cyrtaucheniidae	9	Corinnidae	10
Dictynidae	1	Ctenidae	4
Dipluridae	1	Cyrtaucheniidae	4
Gnaphosidae	24	Dictynidae	1
Hersiliidae	1	Dipluridae	1
Heteropodidae	1	Gnaphosidae	32
Idiopidae	4	Hahniidae	1
Linyphiidae	3	Hersiliidae	1
Lycosidae	11	Heteropodidae	3
Nemesiidae	2	Idiopidae	7
Ochyroceratidae	1	Linyphiidae	8
Oonopidae	4	Lycosidae	13
Oxyopidae	3	Mimetidae	1
Palpimanidae	5	Miturgidae	5
Philodromidae	5	Mysmenidae	1
Pholcidae	4	Nemesiidae	1
Prodidomidae	14	Ochyroceratidae	1
Salticidae	26	Oonopidae	8
Scytodidae	1	Oxyopidae	9
Segestriidae	1	Palpimanidae	4
Selenopidae	1	Philodromidae	6
Sicariidae	1	Pholcidae	3
Theraphosidae	1	Prodidomidae	4
Theridiidae	1	Salticidae	31
Thomisidae	3	Segestriidae	2
Zodariidae	9	Telemidae	2
Unidentified	1	Tetrablemmidae	1
		Tetragnathidae	1
		Theridiidae	14
		Theridiosomatidae	1
		Thomisidae	15
		Uloboridae	1
		Zodariidae	17
Total species	151	Total species	229
Total families	34	Total families	40

ly typical of those found in earlier studies of semi-arid savannas elsewhere in Africa (Russell-Smith 1981, Russell-Smith et al. 1987, Lotz et al. 1991). In all of these areas, gnaphosids and salticids are among the most diverse families, with the former apparently dominating drier sites and the latter more species rich in somewhat higher rainfall areas. In the very humid savanna at Lamto, Côte d'Ivoire (mean annual rainfall 1300 mm), salticids accounted for 19% of all species and gnaphosids for only 6.7% (Blandin & Celerier 1981). Other species rich families in previously studied sites include Zodariidae (4.8–

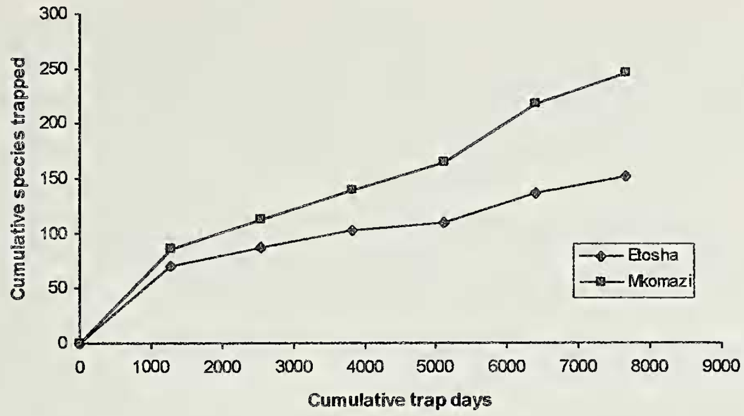

Figure 1.—Cumulative numbers of spider species trapped in Mkomazi Game Reserve (Tanzania) and Etosha National Park (Namibia).

12.8% of all species) Lycosidae (8.5–21.5%), Oxyopidae (2.1–5.7%) and Thomisidae (3.3–17.0%). However, the results differ from those of Whitmore et al. (2002) who found that gnaphosids represented only a small proportion of the total spider fauna of a savanna area adjacent to Kruger National Park in South Africa. They suggest that this was probably a result of the very high level of disturbance of pitfall traps by baboons (Whitmore, pers. comm.).

If it is assumed that the difference in spider species richness between Mkomazi and Etosha is real rather than an artifact of undersampling, what factors might account for the difference? There are at least three possible explanations, none of which are necessarily mutually exclusive: a) a latitudinal gradient in spider diversity exists, with highest diversity at the equator and decreasing diversity with increasing latitude; b) spider diversity is related to mean annual rainfall, with higher diversity in wetter areas; c) there are unique differences in the regional pools of available spider species in the two regions which determines the diversity in each area. There is some support for the concept of a latitudinal gradient of diversity of spiders, at least between the equator and the northern hemisphere. For example, Weselowska & Russell-Smith (2000) present empirical evidence for an area-specific decline in species richness of salticids between Mkomazi (4° S) and the UK (~ 55° N) of approximately one order of magnitude, although there are insufficient data sets from Africa to place very great reliance on this conclusion. However, Platnick (1991) has suggested that there is little decline in diversity of spiders between the equator and southern latitudes of the neotropical region, although without supplying comparative data to support the contention.

Although the range of annual rainfall in the two areas studied overlaps (see site descriptions above), there is little doubt that Etosha National Park is, overall, considerably more arid than Mkomazi Game Reserve. Much of the former has annual rainfall of less than 400 mm and complete failure of annual rains is a regular, if infrequent occurrence. By contrast much of Mkomazi, including the areas in which most of the pitfall trapping was conducted, has annual rainfall above 550 mm, and here complete failure of both the short and long rains is extremely rare. Some support for the importance of rainfall in determining ground-active spider richness can be seen in the relative proportion of gnaphosoid species (Ammoxenidae, Gnaphosidae and Prodidomidae) in the two areas, 29% of the total in Etosha and 16% in Mkomazi. Evidence from studies of other savanna sites in Africa does suggest that gnaphosids are characteristically more diverse in more arid sites while the reverse applies to salticids.

A final possibility, that there is a large difference in the size of the regional pools of spider species from which the fauna of the two areas was drawn, is more difficult to establish. That there are differences in the ocurrence of spider families represented in the two regions seems certain. Thus, Griffin (1998) does not include Tetrablemmidae, Telemidae, Cyatholipidae and Symphytognathidae in her list of spider families recorded from Namibia while all are recorded from Tanzania. Conversely, Ammoxenidae are well represented in Namibia but are known to be absent from East Africa. However, none of these families contributed many species to the total from either area studied and it is probably the size of the regional pools of species in the more diverse families, such as Salticidae and Gnaphosidae, that is more pertinent here. Unfortunately, the systematic data for any of the larger families of spiders in any region of Africa is currently woefully inadequate. As an example, among the 69 species of salticids recorded from Mkomazi Game Reserve, nearly half were found to be new to science (Weselowska & Russell-Smith 2000). Until the systematic understanding of the larger spider families in Africa is greatly improved, it is difficult to assess how far the size of regional species pools effects spider diversity of specific areas.

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